SOME EVOLUTIONARY FEATURES INHERENT IN THE INSECT FAUNAS OF THE TROPICS

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This preliminary statement is of very general nature, designed to present views developed over many years, most recently as the result of a prolonged sojourn in the Philippines. I have been persuaded to present it after reading a very illuminating paper on Evolution in the Tropics by the distinguished geneticist, Dobzhansky (1950).

Is there more variety and specialization in the insect fauna of tropical countries than in more temperate regions? Is the "exhuberance" of life really greater, or is this only our own viewpoint since the insects of temperate regions have been longer known and accepted as commonplace?

If variety is greater, is this due to more active metabolism at higher temperatures, to a longer active season, or to keener competition with other insects, animals or plants?

Such questions have intrigued me for many years, and I have been unable to accept wholly any of the specific pronouncements made by entomologists and other biologists concerning its several phases. The abundance of insect life is regulated by food-supply, reproductive potential and disease, including the depredations of parasitic and predatory enemies, as well as non-living factors in the environment. Aside from the present status, there is also an historical aspect dating back into their geological history. This is complex and cannot be evaluated with our present knowledge of the ecological relations, abundance and migration of special types during the long period that insects have existed in practically the same variety that they now exhibit.

During the past several decades I have had the opportunity to visit a number of tropical areas for periods extending over several months or more. These include Jamaica, Cuba, the Windward Islands and equatorial South America in the Neotropical Region, and several parts of the Indomalayan Region. These personal experiences serve to supplement information gained from other sources.

Viewed critically from a morphological, ecological and behavioristic standpoint, and restricting consideration to insects alone, the following statements seem to be well justified.

There exists a greater variety and more extensive specialization in the insect faunas of the tropics, except with regard to some types of ecological adaptation such as cold hardiness. The difference is by no means so striking as appears at first sight to a visitor from one of the north temperate countries who finds the face of Nature strange and unexpected in any tropical environment. Nevertheless, more extended familiarity with any tropical insect fauna seems never to erase this first impression.

Whether the tropical fauna is as a whole more numerous in genera, species and individuals remains a separate and more difficult question to answer with complete assurance, since our knowledge of the two areas is not coordinate. It seems, however, that the long series of species that are rarely seen or collected is larger than that met with in temperate climates. Also, from the standpoint of climate, the warmer regions are most hospitable to insect life and these include several widely separated very extensive faunas and many faunistically isolated, but smaller areas. None seems to have suffered comparatively recent catastrophic disturbances such as the extensive glaciation of northern faunas.

In spite of the opportunities, there does not seem to have been the same rapid dissemination of insects by artificial means in the tropics as in the north temperate world. The south temperate regions are of course far less extensive and less disturbed by the march of civilization so they offer little confirmation for any generalizations at the present time. Some insect pests are tropicipolitan but these are mainly semi-domesticated species such as cockroaches, flour-beetles and mosquitoes. This dissimilarity may be only apparent as large-scale cultivation in tropical countries is not yet in full operation and more extensive migration may follow rapidly in the future. It is already notable in the case of various trypetid fruit-flies and scale insects. In this respect tropical insects appear to differ radically from tropical weed-plants as an excessive number of the latter seem to have girdled the globe magnificently; no more widely, however, than some of their temperate region counterparts.

Taking all such matters into consideration it appears that no

conclusion can be drawn with certainty, but it may be said that tropical insects are more intimately dependent upon exact environmental conditions, particularly in the struggle for existence with competing species, and with their enemies, most of which are other insects.

What has been commonly termed "the exhuberance of life" in the tropics does not apply to warm-blooded animals like ourselves, and perhaps partly for this reason, has appealed to many naturalists, particularly since the time of Darwin and Wallace. Such peculiarities as the outrageously modified pronotum of certain tree-hoppers and the bold, contrasting color patterns of fishes are to be cited in this category. We may, of course, note similar modifications in the hypertrophied ovipositor of certain parasitic wasps in our region, but the latter are clearly to be considered as functionally useful adaptations. Such exhuberance seems to withstand critical examination as a general phenomenon and to represent one of the trends of evolution in the tropics to which I wish to call attention at this time. It finally came to mind most forcibly during a recent sojourn in the Philippines, where we spent nearly a year on Negros Island. As is often the case on tropical islands, there are foothills which edge the coast and rise to higher elevations further inland where they culminate in mountain peaks. These latter rise to a height of over 6,000 feet toward the interior of the island, and as the result of meteorological conditions, are clothed with a jungle of perpetual rain forest above an elevation of about 4,000 feet. The mountainsides are furrowed by deep ravines and suitable areas below 3,000 feet are cultivated irregularly amid an overall growth of weeds that range from coarse grasses to shrubs and are in great part intruders from other tropical floras.

As we gradually became acquainted and grew more familiar with the insect fauna of the foot-hills and the upper reaches of the mountains there was evidence of a prevailing low density in the insect population. One group of insects failed completely to fit into this picture, however. Ants of many kinds were far more abundant than we had previously noted in any other area, even in the tropics. On the whole, ants are a dominant group of insects in practically all regions under the most varied environmental conditions, but both their abundance and variety is clearly enhanced in warm, and especially tropical, regions. This is particu-

larly true of the predatory forms. Ordinarily these are not very prolific, producing small colonies and not affecting to any great extent the prevalence of small animals, mainly insects, on which they feed. Outstandingly among predatory ants are the members of the subfamily Dorylinae, represented in the tropics by the driver ants of the genus Eciton in America and by Dorylus and Ænictus in the African and Indomalayan regions. These ants are among the most rapacious of all insects, forming very populous colonies whose members scour the vicinity of their nests for insect food and, moreover, migrate widely and at frequent intervals in order to encompass fresh hunting grounds.

Other ants that occur in excessive abundance in many parts of the American tropics are the large leaf-cutter ants of the genus Atta whose colonies are probably the most populous of any ants, but these feed exclusively on fungi cultivated on a vegetable substratum in subterranean mushroom-gardens and do not affect the general insect fauna except in an indirect and very minor way. The same relationship prevails to a lesser but very considerable extent among the more abundant types of ants in temperate regions. Many such appear to select their food primarily on the basis of its saccharine content as they are particularly enamoured by sweets, either directly from a plant source or through the intermediary of aphids, coccids, membracids, food pantries, or the like. Their appetites often extend to other types of vegetable food, but rarely to the living tissues of green plants, except the seeds which form the diet of many graminivorous ants. Dead insects are attractive and freshly pinned specimens of insects must be protected from many small ants in all parts of the tropics. This attraction extends also in some cases to living insects. One little species of Dolichoderus in the Philippines commonly invades cages housing caterpillars or even large, powerful mantises, swarming over them in such incredible numbers that death may ensue within a few hours. This same ant is commonly seen running in long files on the porches and sills of houses, and appears to be a quite general feeder.

A greater intensity in the struggle for existence is the factor which has generally been invoked in connection with the greater specialization and bizarre structural modifications that appear more commonly among the insects of tropical faunas. That it is

related to the phenomenon of "exhuberance", as mentioned previously, seems very likely and if so, it should be possible at least to surmise what the relationship may be. It is quite naturally assumed that there is some effect of higher temperatures in stimulating greater metabolic activity among cold-blooded animals like insects. This is borne out by the presence of numerous insects in the tropics which are conspicuously larger than those of colder climates. We cannot question the truth of this difference as it prevails in a number of unrelated types native to several faunal areas.

It must be admitted that there appears a paradoxical situation among numerous cold-blooded marine invertebrates of our northern Pacific coast where they are represented by a series of species of unexpectedly large size. This seems attributable to a superabundant supply of plankton-food persisting over a long period, and not comparable to the phenomenon just cited.

Another matter which may seem somewhat irrelevant is a peculiarity of the greatly limited fauna of an oceanic island like Hawaii, where two genera, one a weevil and the other a parasitic wasp, have each developed some one hundred species, although these genera are practically confined to Hawaii. This is a case of elaborate speciation, perhaps associated with a lack of competition with other insects, as the native fauna of Hawaii is very limited, lacking a great many widespread groups of insects. Similar cases occur among snails, but not always on isolated islands. Such extensive speciation occurs in certain genera of insects sporadically in all parts of the world and it would appear that such speciation cannot be attributed to any single extraneous stimulus.

It has been generally assumed that the conditions involved in the phenomenon of tropical exhuberance are present in the environment, but whether they pertain to the animate or to the inanimate world, or to both is an open question.

Since insects are as a group the most abundant and diversified of all specialized animals, we may look at the components of the insect fauna itself for indications as to what part they may take in furthering or hindering the evolution of the other components which make up the whole.

I am satisfied that inquiry along this line brings to light one comparatively small group, comprising a single family among the

several hundred into which taxonomists divide the insects, that has played a major role in the evolution of many other types. There are the ants. We cannot say with assurance why these are more abundant in the tropics, nor why the predatory forms of ants are better represented in such warm climates. That a temperature factor is concerned seems likely. As a group they enter, particularly the predatory forms, into the struggle for existence among a great variety of other insects, and as a result of their highly integrated social habits possess a powerful advantage over most other forms of insect life. A far larger proportion of ants serve as important enemies of other insects in tropical countries than they do elsewhere. Also, the influence of the ants is reflected in other ways not related directly to inimical contact with other insects.

This is patent among myrmecophilous insects of many groups. Their peculiarities are both structural and behavioristic and their development as the direct result of association with ants has never, and cannot be questioned. Myrmecophily is world-wide and reaches its most conspicuous development in the tropics. It is prevalent among both predatory and other ants, but reaches its peak with the highly predatory doryline ants in both the new and the old world tropics.

The results of contact between ants and plants are shown likewise in the appearance of many very remarkable modifications among varied types of flowering plants. These are conspicuous in the Neotropical, Ethiopian and Indomalayan regions and we may mention Cecropia, Triplaris, Acacia, Myrmecodia, Hoya and many others. The two latter genera are common in the Philippines where both are excessively modified and adapted as nesting sites for particular kinds of ants.

In other words, the ants have stepped up the speed of evolution among other insects in the tropics quite generally.

Reference

DOBZHANSKY, THEODOSIUS.
1950. Evolution in the Tropics. *American Scientist*, 38(209-221).